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论平当树属的系统位置

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ON THE SYSTEMATIC POSITION OF *PARADOMBEYA* STAPF

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摘 要 在现代植物分类系统中，平当树属被归入梧桐科或木棉科，其正确的系统位置至今没有定论。本文从外部形态、幼苗形态、脉系、叶和木材及种皮解剖、花粉形态及染色体数目等诸方面对该属进行了研究。在平当树属中，花排列成聚伞花序，果成熟时花被宿存；雄蕊 15, 5束，与5枚退化雄蕊结合成雄蕊筒，花药2室；子叶2裂；等面叶，中脉维管束2, 弓形，叶柄维管束2, 圆形；气孔器限于下表皮，不等细胞型或稀短平列型；外种皮 5— 6层细胞厚，内种皮 3— 4层细胞厚；导管分子弦向直径 54— 83μm, 长 270— 423μm, 复管孔常由 10— 20个管孔组成，排列成显著的径列管孔链，管孔很多，轴向薄壁组织极少，射线单列或2— 3列，异型；花粉粒具3孔，球形，外壁具刺；体细胞染色体 2n=20, 核仁在有丝分裂前期消失。根据上述特征及其与梧桐科和木棉科的比较，作者认为平当树属应该属于梧桐科的 Dombeyeae 族，不宜移至木棉科。

关键词 平当树属；系统位置；梧桐科。

Abstract The systematic position of *Paradombeya* Stapf has been debated until now. The studies on gross morphology, anatomy, palynology and cytology were undertaken to confirm the systematic position and affinities of this genus. The combination of features, e. g., umbel−like cyme, 2−celled anther, presence of staminodes, staminal tube, 15 stamens, bifid cotyledons, wood anatomy, chromosome number of 2n=20, triporate, spiny and spheroidal pollen grains, suggests that the genus be better placed in the tribe Dombeyeae of the Sterculiaceae.

Kew words *Paradombeya;* Systematic position; Sterculiaceae

Introduction

The genus *Paradombeya* Stapf, with 2 or 3 species, is distributed in Burma, Thailand and Southwest China. The distribution pattern might indicate its relic nature.

Paradombeya Stapf was established in 1902, based on the type species *P. burmanica* Stapf from Upper Burma, as a member of the tribe Dombeyeae of the Sterculiaceae, and the affinities with *Corchoropsis* Sieb. et Zucc. and *Pentapetes* Linn. were pointed out. In Dalla Torre and Harms' Genera Siphonogamarum (1900— 1907), it was treated so, but

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in " Register zu Dalla Torre－Harms Genera Siphonogamarum" (1958), it was treated as a member of the family Bombacaceae instead. In the current classification systems, *Paradombeya* Stapf is treated as a member of either the Bombacaceae (Airy Shaw 1973, 1985; Cronquist, pers. comm.) or the Sterculiaceae (Hutchinson 1967; Takhtajan 1987). Then a question arises, which family does this genus naturally belong to. In order to answer this question, studies on gross morphology, anatomy, pollen morphology and cytology were undertaken in the present work.

Materials and Methods

Except pollen materials taken from herbarium specimen (Li H. W. 285), all materials of *Paradombeya sinensis* Dunn were collected by the author in Shiping County, Yunnan Province. The voucher specimens are deposited at KUN.

Leaves and petioles were fixed in FAA. Transverse sections (6— 10μm) of leaves and petioles were prepared according to the conventional paraffin method, stained with safranin and fast green. The dried wood samples were boiled in water in order to soften the wood. Transverse, radial and tangential sections were cut into 6— 12μm thick, stained in safranin. Epidermal peels were taken from leaves treated with 10% NaOCl, regularly dehydrated, stained in safranin. For chromosome observation, root tips from germinating seeds were pretreated in 0.002 mol/L hydroxyquinoline for 45— 60 minutes, fixed in Carnoy's fixative for 4— 8 hours, macerated in 1 mol/L HCl at 60℃ for 8— 10 minutes, stained in Carbolic fuchsin, and squashed in 45% acetic acid. Pollen grains for light microscope observation were treated according to Erdtman (1952), and mounted in glycerlin jelly, those for SEM examination were directly coated with gold before observation.

The terminology used in the anatomy, wood, pollen and leaf venation follows Metcafe and Chalk (1950), Tang (1982), Erdtman (1952) and Kremp (1965), and Hickey and Wolfe (1975), respectively.

Observation and Results

Morphological description (Fig. 1)

Shrub, or rarely small tree. Leaves simple, alternate, stipules 2, deciduous. Flowers bisexual, in axillary umbel－like cyme of 3— 6 flowers, yellow, 1— 3 cymes fascicled in an axil, bracteoles 3, verticillate, caducous; calyx 5－partite, segments valvate; petals 5, imbricate; fertile stamens 15 in 5 clusters alternate with 5 ligulate staminodes, both fused at the base into a short staminal tube, anther ovate or elliptic, basifixed, glabrous, 2－celled, longitudinally dehiscent; ovary sessile, superior, spheroidal, densely stellate－tomentose, 5－or 2－locular, placenta axile, loculi 2－ovuled, ovules ascending, style subulate, simple. Capsule loculicidally dehiscent, 2－or 1－seeded, enclosed by

persistent perianth; seeds small, with copious endosperm and foliaceous bifid cotyledons. Indumentum stellate.

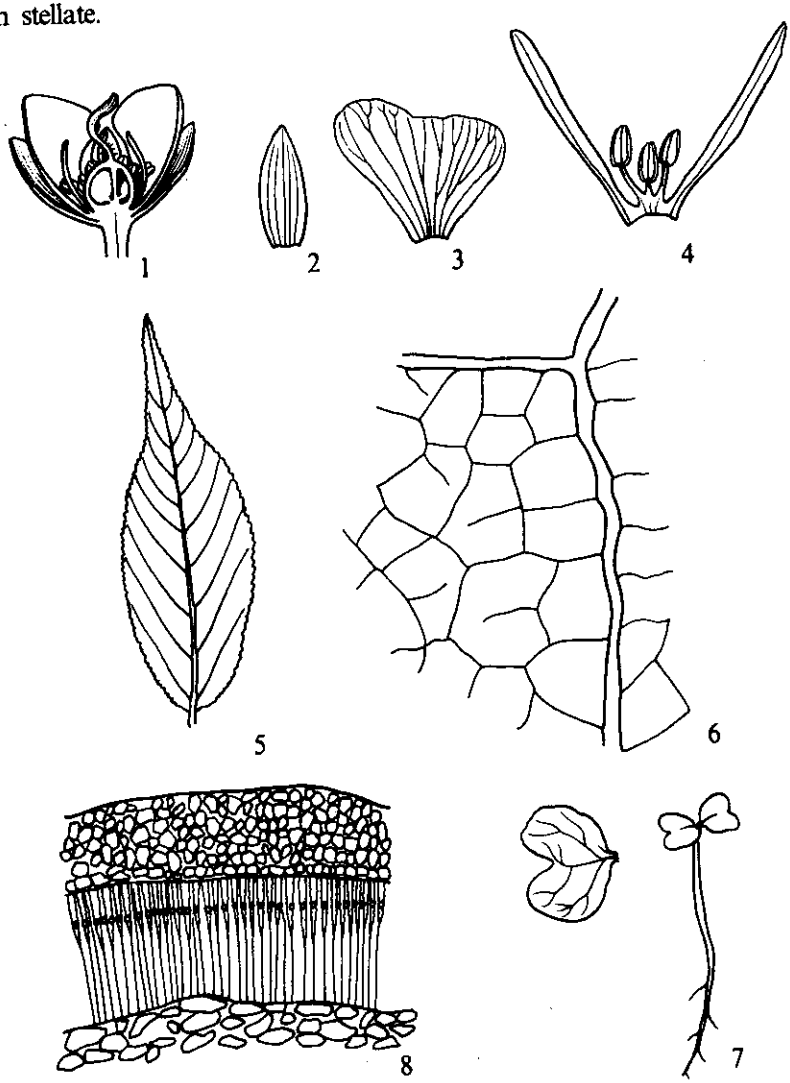

Fig. 1 1. Longitudinal section of flower; 2. Sepal; 3. Petal; 4. A group of stamens with staminodes showing the fusion of stamens and staminodes; 5— 6. Leaf venation, 5×0.8, 6×65; 7. Seedling showing 2-lobed cotyledons; 8. Seed-coat, × 375.

Anatomy (Plate 1, Plate 2, Plate 3: 15— 16)

Leaf: In the cross section of lamina, the upper epldermis is one-celled in thickness, cells rectangular, densely and regularly arranged, in which mucilage cells present. The lower epidermis is similar to the upper one but cells are smaller and more mucilage cells are present. Mesophyll is composed of palisade cells, the uppermost two layers regularly and densely arragned, and other layers slightly loose. The vascular bundle of midvein consists of two bundles, bicrescent or arc-shaped in cross section, the abaxial one is

larger and more incurved than the adaxial one. Rhomboid crystals are present in parenchyma of phloem and other parts. In cross section of petiole, epidermal cells are densely arranged and a number of mucilage cells were found mixed with epidermal and parenchymatous cells. The vascular bundle exhibits a closed ring enclosing one small central ring.

In surface view, epidermal cells are tetra-or pentagonal, subisodiametric or anisodiametric, anticlinal wall slightly sinuous on the lower surface, stomatal apparatuses are confined to the lower surface, mostly of the anisocytic, or rarely of the paracytic, type.

Leaf venation (Fig. 1: 5— 6): venation pinnate, with a single midvein following a straight unbranched course. Midvein of moderate size. Secondary venation nearly craspedodromus, with an acute angle of divergence, nearly uniform for all secondary veins. Relative thickness of the secondary veins moderate. Tertiary veins following an orthogonal course. Ultimate veinlets simple, linear. Areoles regular, moderately developed and oriented, predominantly quadrangular, rarely quinquangular or triangular. Teeth simple, glands absent.

Wood (Plate 2, Plate 3: 15— 17): Growth ring is apparent. Pore groups form predominantly radial pore chain of 3— 45, each usually with 10 to 20 cells, very occasionally tangential or in cluster; pore chains are regularly arranged; pore outline is transversely elliptic or subrounded, tangential pore diameter ranges from 54— 83 μm, with an average of 60 μm. Vessel element length averages 355μm, with a range of 270— 423μm. Intervascular pitting is alternate, 3.2μm in diameter. Pits to rays are similar to intervascular pitting, Tyloses are occasionally present. Vessel element end wall angle is about 45°. The pore number per sq. mm. ranges from 109 to 154. Vascular rays are of two distinct sizes, heterogeneous (Kribs Heterog. I or IIB), both uniseriate rays and 2— 3 cells wide rays numerous. Even the three-seriate rays are norrower than pores in transverse section; uniseriate rays are 4— 12 or more cells high, cells appear oblong in tangential section, multiseriate rays are 22— 44 or more cells high, cells are subelliptic in tangential section. Xylem parenchyma is very poorly developed. Fiber length ranges from 745 to 1275 μm, obviously storeyed, fibre wall is thick, pits small. Compared with the above features, a shrub sample presents some variation: tile cells numerous, multiseriate rays 2— 4 cells wide, slightly shorter vessel elements 255— 434μm long, and smaller pores 37.5— 60μm in diameter.

Seed coat (Fig. 1:8): Testa 5— 6 cells thick, cells of outer epidermis regular, middle layer irregular; tegmen 3— 4 cells thick, cells of outer epidermis obviously palisade, well developed, mesophyll irregularly arranged, more or less collapsed, inner epidermis unspecialized.

Pollen morphology (Plate 3: 18— 24)

Pollen grains spheroidal or prolate, 50— 80μm in diameter, amb circular; triporate

or rarely bi－or monoporate, pores circular; exine thickened around the pores, spiny, spines 4— 6μm long, basally divided. Exine stratification apparent, sexine thicker than nexine.

Cytology (Plate 3: 25— 26)

The chromosome number, 2n＝20, is reported here for the first time for *Paradombeya sinensis* Dunn. The nucleolus disappears normally in the course of nucleus division.

Comparison and Discussion

A. Morphology

Paradombeya possesses a number of morphological characters common to the tribe Dombeyeae in the Sterculiaceae (Table I), whereas it differs from the Bombacaceae in numerous features. In the Bombacaceae, the flowers are usually in fascicles, petals caducous, stamens usually numerous, staminodes absent, anther monothecal, cotyledons entire. Among these characteristics monothecal anther is unique. From the comparison, it can be seen that *Paradombeya* shows fewer similarities to the Bombacaceae than to the Sterculiaceae.

B. Anatomy

In the anatomy of leaf, petiole and seed coat, *Paradombeya* Stapf is similar to both the Sterculiaceae and the Bombacaceae (Dehay 1941, 1942; Inamdar & Chohan 1969; Metcalfe & Chalk 1950; Shanmukha Rao et al. 1981, 1983). The isobilateral leaf and 5— 6 cells thick testa resemble those of some Sterculiaceae (Corner 1976; Metcalfe & Chalk 1950). The tegmen is thinner than that of both families (Corner 1976).

The leaf venation of *Paradombeya* is similar to that of *Corchoropsis*, *Pentapetes* and *Pterospermum* in simple, linear veinlets, simple teeth, gland absence, orthogonal quaternary and quinternary veins and other features.

With respect to wood anatomy (Table II), *Paradombeya* possesses some features agreed with the Bombacaceae (Metcalfe & Chalk 1950): simple perforation plate, alternate intervascular pitting, heterogeneous rays. But a number of disagreements between this genus and the Bombacaceae are present. In the Bombacaceae, pores 0.5— 5 per sq. mm. dominantly solitary, or very rarely multiples of 2— 3 cells, parenchyma well developed and even forming ground tissue, multiseriate rays 4— 10 cells wide, 2— 12 per. mm., uniseriate rays very rare. On the contrary, in *Paradombeya*, pore groups are in obvious radial chains composed of 2— 45, usually 10— 20 cells, and very numerous, parenchyma very scanty, uniseriate rays 2— 3, rarely 4 cells wide, multiseriate rays numerous. The Byttnerioideae of the Sterculiaceae share some features with *Paradombeya*. In the Byttnerioideae, pores small (50—100μm) in some genera, such as *Reevesia*, *Scaphopetalum* and *Theobroma*, multiples of 4 or more cells common in *Dombeya*, *Eriolaena* (Metcalfe & Chalk 1950), of 20 cells present in *Physodium* and *Some Melochia* (Dorr & Barnett 1989), obvious

Table I Morphological comparison of *Paradombeya* with related taxa

Character	*Paradombeya*	Dombeyeae	*Durio*	*Hampea*	*Matisia*	*Catostemma*	*Bombax*	*Ceiba*
Flower	axillary	axillary	?	axillaly	lateraty	axillary	axillary	axillary
Inflorescence	cyme	cyme	fasciculate	subfasciculate	fasciculate	fasciculate	fasciculate or solitary	solitary or fasciculate
Petal	5, marcescent	5, marcescent, very rarely deciduous	5, deciduous	5, deciduous	5, deciduous	5, deciduous	5, deciduous	5, deciduous
Stamen	15, 5 groups	5— 20, 5 groups	numerous	numerous	numerous	numerous	numerous	10— 15
Anther	2−celled	2−celled	1−celled	1−celled	1−celled	1−celled	1−celled	1−celled
Filament	fused at the base	fused at the base	free or united at the base	united at the base	united at the base	free or shortly united at the base	united at the base	united at the base
Staminode	5	5, rarely 0	0	0	0	0	0	0
Arrangement of stamens and staminodes	one whorl composed of 5 stamen groups & 5 staminodes	similar to that in Paradombeya or rarely absent	absent	absent	absent	absent	absent	absent
Ovary	5−or 2−locular	5−locular	5−locular	3−locular	5−locular	3−locular	5−locular	5−locular
Fruit	capsule	capsule	capsule	capsule	capsule	capsule	capsule	capsule
Cotyledon	foliaceous, bifid	plicate or foliaceous, 2−partite	flat−convex	contorted−plicate	corrugated	?	foliaceous	contorted-plicate
Leaf	simple, pinnate-nerved	simple, pinnately or palminerved	simple, pinnate-nerved	simple, palminerved	palminerved	1−foliolate, pinnate−nerved	digitately foliolate, pinnately nerved	digitate, pinnate−nerved
Habit	shrub, rarely small tree	shrub, rarely tree or herb	tree	small tree	tree	tree	tree	tree

Table II Comparision of wood anatomical feature

Character	*Paradombeya*	Bombacaceae	Sterculiaceae
Pore diameter (μm)	38— 83	100— 200 or more than 200	100— 200, less often 25— 100
Pore group	remarkable radial pore chains of 10— 20 cells	solitary or multiple of 2— 3 cells	solitary or in small radial multiple of 4 or more cells
Pore/mm^2	85— 154	0.5— 5	1— 5— 75— ∞
Perforation plate	simple	simple	simple
Intervascular pitting	alternate	alternate	alternate
Vessel element length (μm)	240— 515	300— 800	200— 500
parenchyma	very scanty	abundant or forming the ground tissue	abundant
Ray	two distinct sizes	two distinct sizes	two distinct sizes
Ray/mm	15	2— 12	4— 20
Uniseriate ray	numerous	not common except for Durioneae	numerous
Multiseriate ray	2— 3(4) cells wide	4— 10 or 10— 15 cells wide	2— 20 cells wide
Ray type	Heterog. I. IIB.	Heterog, IIA, IIB.	Heterog. IIA, IIB.
Tile cell	present, or nearly absent from tree sample	present	present, or absent from Dombeyeae

radial chains present in one genus (Tang 1973), pores very numerous in *Reevesia*, *Fremontiodendron (Fremontia)*, uniseriate rays numerous, multiseriate rays 2— 10 cells wide, perforation plate simple, intervascular pitting alternate.

The comparison shows that *Paradombeya* resembles anatomically the members of the Sterculiaceae, while differs from those of the Bombacaceae in a number of characters.

C. Pollen morphology

The following evaluation of the Bombacaceae is based on Erdtman (1952), Tsukada (1965), Fuchs (1967), Sharma (1970) and personal observation. Pollen grains of the Bombacaceae fall into following categories: I. Tricolporate; exine reticulate. Most genera. II. Triporate; exine spiny or excrescent. A few genera. III. Periporate; exine spiny. Only *Hampea*. Only the second type seems similar to that in *Paradombeya*, and it seems reasonable to place *Paradombeya* in the Bombacaceae. In the Bombacaceae, however, the systematic position of the taxa with this type of pollen is isolated. Different opinions have been proposed (Fuchs 1967; Singh et al. 1984, etc.). Moreover, these taxa are different from *Paradombeya* in gross morphology.

Based on Coetzee 1979, Cristobal 1968, Erdtman 1952, Hsue et al. 1982, Litchfield 1966, Long et al. 1985, Rao 1950 and personal observations on Chinese taxa, pollen grains of the Sterculiaceae fall into four types: I. Tricolporate, exine reticulate most genera; II. Triporate, angulaperturate or planaperturate, exine reticulate in Helictereae, Byttnerieae; III. Triporate, exine apiny (Dombeyeae); IV. Oligoforate, exine spiny (only Eriolaeneae).

It appears apparent that the only pollen type similar to that of *Paradombeya* is the one in the tribe Dombeyeae, in which the genus *Paradombeya* was originally placed.

The preceding review shows that *Paradombeya* pollen can be completely neither matched nor disagreed with bombacaceous or sterculiaceous pollen. However, besides pollen similarity, the tribe Dombeyeae shares numerous features with *Paradombeya* in gross morphology and this tribe is consistently placed in the Sterculiaceae.

From the preceding discussion, it seems reasonable to retain *Paradombeya* in the tribe Dombeyeae of the Sterculiaceae.

D. Cytology

2n=20 is the only one chromosome number published for this genus. In the Bombacaceae, the commonest chromosome numbers reported are 2n=72 or 144 (Baker & Baker 1968), with the exception of n=14 and 2n=56 in *Durio zibethinus* and *2n=26* in *Hampea rorirosae*. The basic chromosome numbers have been suggested as 36 (Baker & Baker 1968), 12 (Miege & Burdet 1968), 12, 8, 10, 11 (Mangenot & Mangenot 1958). Considering the basic chromosome number of angiosperms (Raven 1975), it might be suggested that the original basic number for this family be x=9. In the Bombacaceae, besides high chromosome numbers, another remarkable cytological feature is the persistence of the nucleolus through nucleus division (Baker & Baker 1968).

The cytological data in the Sterculiaceae (Darlington & Wylie 1955; Cave 1958— 1965; Ornduff 1967— 1969; Moore 1970— 1977; Goldblatt 1981— 1990) are summarized in Table III. In the Dombeyeae, chromosome number counts were reported for three genera, of which *Melhania* is of x=10 (Tang Y. 1992), Pentapetes with 2n=76 and probable x=19. The basic chromosome number suggested for *Dombeya* was 23 (Gazet 1939) or 27 (Poty & Hamel 1968). Considering the counts reported and the basic chromosome number of related taxa, it is suggested that the basic number for *Paradombeya* be 10. It can be seen from Table III, the Sterculiaceae is cytologically characterized by its most frequent basic chromosome number x=10.

From the cytological survey, it becomes clear that *Paradombeya* differs remarkably from the Bombacaceae but agrees well with Dombeyeae of the Sterculiaceae.

Conclusion

From Table IV, the Sterculiaceae (mainly Dombeyeae) share 24, while the Bombacaceae

Table III Genera with chromosome numbers in the Sterculiaceae (from related index)

Genus	2n		n		x	
Abroma			10	11	10	11
Ayenia	20	22		11	10	11
Byttneria	28	26	13	14	13	14
Brachychiton	40				10	
Chlamydocola	42				21	
Cola	40	42			20	21(10)
Dombeya	54	46	30		10	27
Eriolaena			60		10	
Firmiana	40		20		10	
Fremontia	40				10	
Guazuma	16		8		8	
Helicteres	18		9		9	
Heritiera	40	28	20	14	10	14
Hermannia	12				6	
Herrania	20				10	
Ingonia	40				10	
Kleinhovia	20				10	
Leptonychia	20				10	
Mansonia	c.50				25?	
Melhania	60		30		10	
Melochia	18	36	9		9	
Pentapetes	76				19	
Physodium			10		10	
Pterospermum	38		19		19	
Pterygota	40		20		10	
Sterculia	40	36	20		10	
Tarrietia	32				8	
Thomasia	20				10	
Theobroma	20	16	8		10	8
Triplochiton	40				10	
Waltheria	40	24	20	12	10	8
Corchoropsis	20				10	

share only 8 characters with the genus under discussion. The sterculiaceous affinity has been most strongly advocated on account of gross-morphological, anatomical, palynological and cytological characters. The bombacaceous affinity supported by pollen morphology is not substantial because the affinity is represented by pollen morphology of the taxa with doubtful affinities. The inclusion of *Paradombeya* in the Bombacaceae would increase the heterogeneity of that family. Consequently, the genus *Paradombeya* should be included in the tribe Dombeyeae of the Sterculiaceae, just as its author originally suggested.

Table IV Character comparison of Paradombeya with Bombacaceae and Sterculiaceae (mainly Dombeyeae)

	Character	Paradombeya	Dombeyeae	Bombacaceae
Gross morphology	Inflorescence	umbel-like cyme	+	−
	Bracteole	3, caducous	+	−
	Calyx	5-partite	+	+
	Petals	5, unequilateral, marcescent	+	−
	Stamens	15, 3 in each group	+	−
	Filaments	fused at the base	+	(+)
	Anthers	2-celled	+	−
	Staminodes	5, alternate with 5 stamen groups to form staminal tube	+	−
	Ovary	sessile, 2-or 5-locular	+	+
	Fruit	capsule	+	+
Wood anatomy	Pore group	radial pore chains composed of 10— 20 cells	(+)	−
	Pore diameter (μm)	54— 83	(+)	(−)
	Pores/mm	109— 154	(+)	−
	Vessel element length (μm)	270— 423	+	−
	Parenchyma	poorly developed	(−)	−
	Rays	uniseriate or 2— 3 cells wide	+	−
	Ray type	Heterog. I, IIB	(+)	(+)
	Rays/mm	15	+	−
Pollen	Aperture	3-porate	+	(+)
	Exine	spiny	+	(+)
	Shape	spheroidal	+	(+)
	AMB	circular	+	(−)
Chromosome	Chromosome number (2n)	20	(+)	−
	Basic number (x)	10	(+)	−
	Nucleolus	disappear normally	+	−
	Total	25	18+, 6(+), 1(−)	15−, 2(−), 5(+), 3+

+: Character state shared by taxa compared; −: Character state not shared by taxa compared; (+): Character state shared by part taxa compared; (−): Character state more or less shared by taxa compared.

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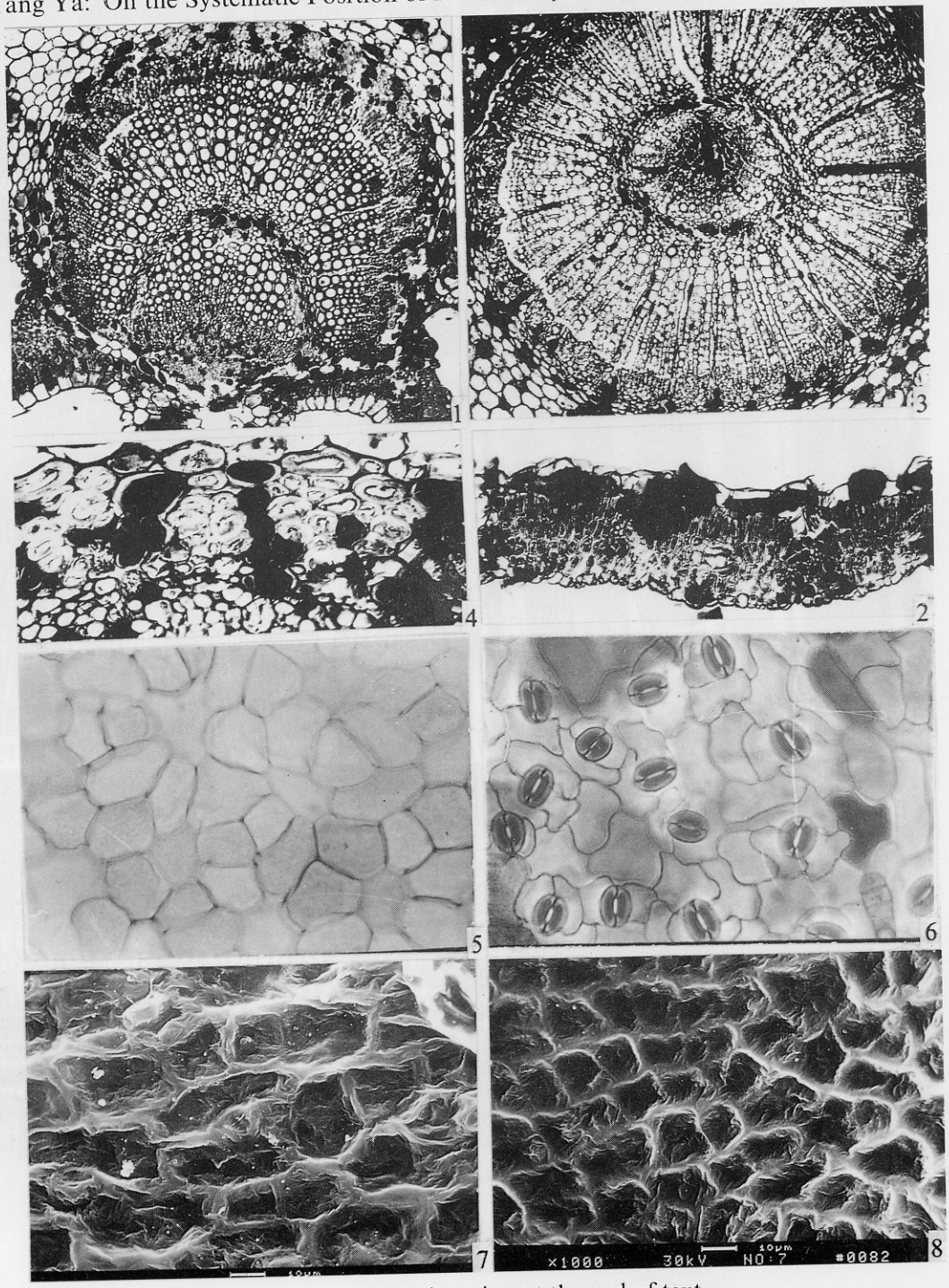
Explanation of Plates

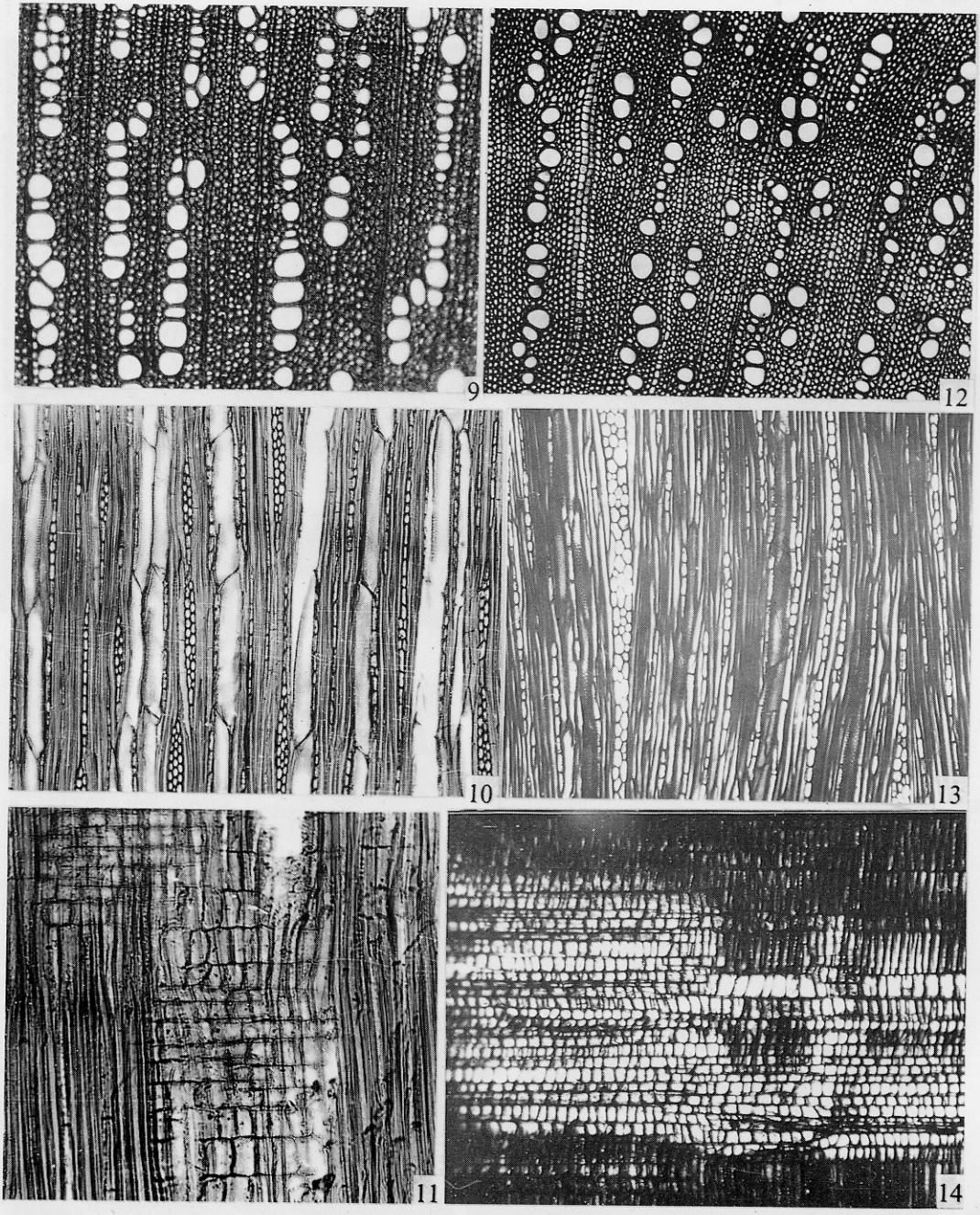
Plate 1 1— 3. Cross-sections of midrib, lamina and petiole of *Paradombeya sinensis* respectively, 1— 2. ×68, 3. ×135; 4. Part of phloem of midrib showing crystalliferous cells, ×270; 5— 6. Upper and lower epidermis of *P. sinensis*, × 320; 7— 8. Surface of seed-coat of *P. sinensis* and *Melhania hamiltoniana* respectively, ×550.

Plate 2 9— 11 Transverse, tangential and radial sections of tree sample of *Paradombeya sinensis*, 9— 10. ×68, 11. ×135; 12— 14. Transverse, tangential and radial sections of shrub sample, all ×68.

Plate 3 15— 16. Radial sections of tree and shrub sample respectively, × 135; 17. Vessel and fibre elements, ×65; 18— 24. Pollen morphology, 4×1500, 18. ×2700, 20— 23, ×400, 24. ×6700; 25. Chromosome, ×3480; 26. Prophase of nuclear division showing disappearing of nucleolus, × 3480.



see explanation at the end of text



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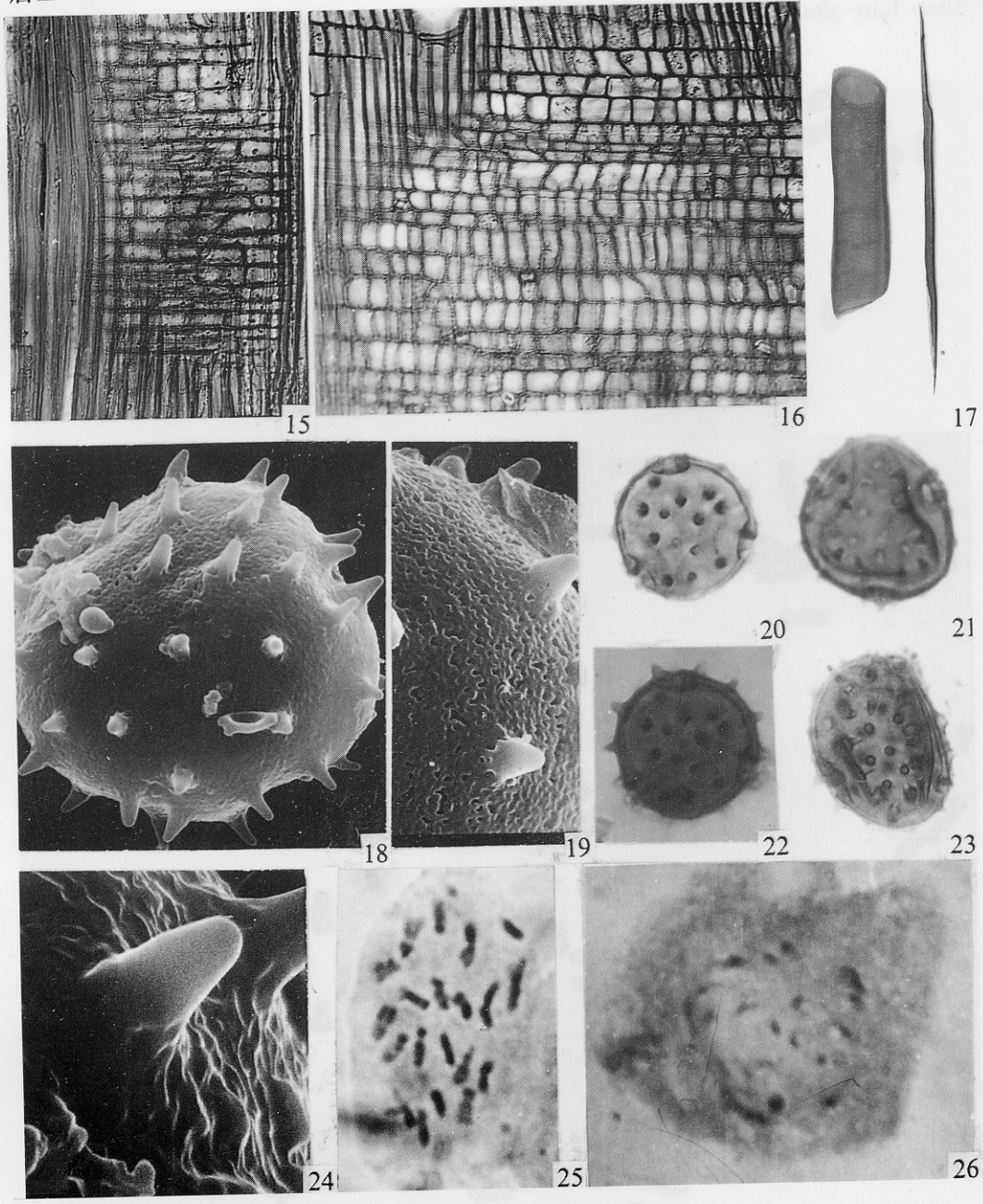

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